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ESTIMATING THE DENSITY OF AN ANIMAL POPULATION

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INTRODUCTION

Obtaining valid data on the number of animals in a population, estimating the density from these data, and determining the confidence limits of the estimates, together are basic to investigations in ecology. Although "good" estimates of population density are highly important (Odum, 1959:150), they are usually difficult to make, particularly among animals as mobile and wary as winged insects and most vertebrates. The problems arising during population estimation have at some time hampered most ecologists, and, hence, efforts to overcome the difficulties have lead to the proliferation of a rather vast literature, which is more or less widely scattered. Therefore, it is proposed to review some important developments in the still rapidly-expanding field of density estimation and to describe a few major procedures that are recommended to insect and vertebrate ecologists. No attempt is made to be "thorough," because that would require a large book, in fact, an encyclopedia. One or more representative types of each of the major kinds of procedures based on sampling of the animals are, however, discussed.

In spite of the fact that obtaining valid data is absolutely prerequisite to the use of density models, methods for obtaining the valid data are not taken up here. The latter would, for one thing, extend the scope of this review to excessive length; and, moreover, each field study is unique to a great extent, requiring usually some unique activities to get these data. Although it is apparent to all that no amount of tedious analysis gives useful results when the data are biased and the bias cannot be removed, yet most of us are too prone to assume that satisfactory data has been obtained, especially when an equation is used to manipulate the figures. Analysis of several kinds of data, used in several different mathematical models, should of course lead to results that approximately agree. If they do not, further

information should be collected and analyzed by the same and other methods to obtain convincing evidence of the most probable density. Good data are the heart of density estimates!

Excellent general reviews of the methods for obtaining the figures and analyzing them, with special reference to vertebrates, have been published by Ricker (1958), Davis (1963), Scattergood (1954), and others. Of special interest to entomologists is the fine book by Southwood (1966); the first 228 pages are on estimating population density, both in an absolute and a relative sense, and considerable is given on how to obtain the data. This book and one by Ricker (1958) are the two best publications available today on the subject of estimating population density of animals, but due to its younger age and emphasis on insects, the book by Southwood is the most valuable publication on the subject for entomologists. Andrewartha (1961), Menhinich (1963), and others have published shorter reviews (but good ones), with emphasis on the insects. Detailed reviews dealing with some restricted groups of methods have been provided by Chapman (1955), Hanson (1963), and others. In his review, Davis (1963:91) pointed out that the supposedly large number of sampling methods for determining the number of animals actually rest on one of three basic classes of enumeration, either (a) true censuses of the whole population, (b) sampling of the animals themselves (rather than of their sign), or (c) indices to the population, involving either the animals or their sign. (Indices are of course the ratio of the number of animals seen to the number of some unrelated kind of object, such as the number of butterflies seen per mile of roadside; or the number of tracks per linear unit of pond margin, or the number of an insect's eggs per leaf of certain plants, etc.).

Concerning the three general classes of enumeration, true censuses are in actual practice rarely attempted because of their excessive cost and because some of the animals may escape counting. Ideally, a true census is most practical when the animals are large and live in habitat where they are easily seen; on the treeless plains of North America and Africa, big game are thus sometimes censused from aircraft, but even then the areas covered are frequently not large. For the average ecologist, a true census of a whole population, or even a small segment of it, is usually out of the question.

On the other hand, indices are often highly feasible and yield valuable information, but that information hardly ever can be converted into estimates of population density. In many prac-

tical investiagtions, it is enough to know that a population has increased or decreased by a certain amount, relative to some long-time set of indices, and thus a mere trend in density, rather than the absolute population density itself, is sufficient. Very often, however, the investigator needs to know more, and thus he is forced to turn to sampling, the random counting of some fraction of the population, and the subsequently extrapolating to the whole population. All further material in this paper will deal with sampling of the animals themselves.

The sampling techniques turn out to be of four general types: (a) a count of all animals on sample plots of known size, (b) marking, release, and re-observing of animals, (c) changes in catch-per-effort or changes in sex or age or other ratios caused by removal of a known number of animals, or (d) analysis of statistical properties of the data's distribution.

Moreover, regardless of the basic class of sampling employed, it nearly always requires a total count of some population component. Even in the mark-and-recapture method, while one component is being made recognizable by marking it, the observer ends up, in effect, making a total count of the marked group and must use this total in later computations. Regardless of how the total count of a population component is obtained, much effort will usually be required, and in many cases the data may still contain biases. In certain situations the work may be restricted by well-known difficulties, such as trap-shyness of the animals, loss of marks, natural segregation of animals by sex or age, uncertainty that all animals on sample plots have actually been seen, ingress and egress from study areas, and many other problems. Now, some of the principal methods based on sampling of the animals (not of their sign) will be described.

TOTAL COUNTS ON SAMPLE PLOTS

In this well-known method of estimating population density, some fraction of a study area is sampled intensively and the results are extrapolated to the total area. The major assumptions behind the method are: (a) The animals are sampled at random, and (b) all of the animals existing on each plot are counted, but are counted only once. The method presents relatively little complexity from the standpoint of analyzing the data, but obtaining reliable data is often quite difficult, especially for insects that are more or less hidden or inaccessible, either in plants,

iin the soil, inside of other animals that are being parasitized, etc. Southwood (1966:99-228) has devoted the majority of his material on estimation of density to the matter of total counts on sample spaces and has given a fine treatment of methods for collecting the insects or otherwise getting the required data.

As usual, the investigator will want to find the mean number of animals seen on the sample plots, $\bar{x}$, and the variance of the sample mean, s^2. From these, he should calculate the confidence limits of his estimated total population, $\hat{K}$. Thus, if he estimates that 50 animals (as in an insect population) are present per sample plot but that the 95% confidence limits are $\pm$ 10, then the true value should be between 40 and 60 of the insects per plot. Moreover, if the investigator has sampled only 1% of the total study area, then the estimated abundance on the whole study area, $\hat{K}$, ranges from 100 times 40 to 100 times 60; that is, $\hat{K}$ would lie between 4,000 and 6,000. Let us now return to the major assumptions underlying the procedure.

To sample the animals at random, the observer samples the area at random, and assumes axiomatically (not requiring further proof), that this leads to a random sample of the animals. Ecologists have frequently pointed out (see Cole, 1946, for example) that animals are seldom distributed at random. Will this negate attempts to obtain a random sampling? When the animals are highly clumped, most of the sample plots will be "blanks," i.e., have no animals on them, while a few of the plots will have a great many animals. Nevertheless, one can still take a random sample of the animals by making a random sample of the study area — because plots with animals and plots with blanks should be encountered with a frequency that corresponds to their frequency over the entire geographical extent of the study area. At least that is the statistical expectation when the work is done properly. This is most important. Some ecologists have claimed that statistical theory is automatically invalid when animals are not spatially distributed at random, but such ideas are, to put it tritely, "highly erroneous." Clumping of animals does not necessarily invalidate statistical theory, but the presence of many plots with no animals and a few plots with many animals does lead to a high variance that results, finally, in wide confidence limits for the estimate of mean density of the whole population.

The data may form (a) a (positive) binomial distribution if each animal has the same probability of being observed, if this probability is not too small, and if the counts of the animals are

independent, i.e., if the observations have no clumping or "contagiousness." The data may form (b) a Poisson distribution if the same conditions hold except that the probability of observation is very small, actually a more common possibility in extensive surveys rapidy conducted over larger areas. (Nevertheless, in total counts on sample plots, the observer is determined to find all or nearly all of the animals regardless of how small this probability of observation may be.) The data may form (c) a negative binomial or other distribution if the animals are contagiously distributed, which is a very common phenomena in nature, as indicated above. It is well known that the ratio of variance to the mean, $s^2 / \bar{x}$, indicates the degree of contagiousness of the data. In the (positive) binomial distribution, the variance is less than the mean, in the Poisson the two are equal, and in the negative binomial the variance is bigger than the mean.

Grieg-Smith (1964), Kershaw (1964), and others have discussed the use of the ratio $s^2 / \bar{x}$ for detecting patterns of nonrandomness among plants. Kershaw (pp. 104-108) gave data analyzed by Grieg-Smith and diagrams and a nice discussion showing how the size of the quadrat affects the distribution of the data. As quadrat size is increased, the data for organisms which are actually clumped will show, successively, a random, contagious, and regular distribution. The most marked contagion results when the quadrat size is about the same as the average area of each clump of organisms.

Although the investigator who is trying to estimate the population density of animals from total counts on sample plots requires to keep the variance of the counts fairly low, he is confronted by a dilemma. If plot size is increased; it reduces the variance due to clumping; but at the same time the increase in the size of individual plots often leads to a reduction in the number of plots which can be searched, a factor that increases the variance again.

Hanson and Chapman (in press) proposed that, where clumping was a marked problem, the number of "clumps," i.e. groups, of animals be counted as well as the number of animals in each group because the distribution of the groups should tend to be at random. Laboratory populations of mealworms (*Tenebrio molitor*) were studied from this standpoint, and experimental estimates of their density were improved by counting clumps. Regardless of the procedure that the ecologist hopes to follow, he should of course consult a statistician before planning his

field surveys and at intervals thereafter to modify the surveys as required by problems encountered.

Therefore, the intensity of the sampling that one should do depends on the degree that the animals clump, and the degree of precision required. According to the writer's experience, it is difficult to stimate the density of a population within 20 per cent of its true value, by any practical method, and even this degree of precision usually requires intensive sampling. In fact, Davis (1963:117) said that investigators "will have to spend fantastically greater time and money on estimates than has been done in the past, if they wish to detect changes of much less than 25-50% of the population."

The size of sample that is required to give any desired size of confidence interval is covered by most textbooks of statistics, for example, Snedecor (1946:457). The standard equation for the statistic t is solved for the sample sizes; it may be remembered that the definition of t is

$$t = \frac{(\bar{x} - \mu)}{s_{\bar{x}}}$$

where as usual x is the mean of the sample; μ (mu) is the true, but unknown mean of the whole population; and s is the standard error of the mean, that is to say, $s / \sqrt{n}$. The symbol s refers, of course, to the standard deviation, which is the square root of the variance estimate, s^2. After the expression equivalent to the standard error, $s / \sqrt{n}$, is substituted into the definition for t, the equation is then solved for n, specifically the sample size required in order to achieve any desired level of confidence for any selected permissible error, viz.,

$$n = t^2 s^2 / (\bar{x} - \mu)^2.$$

The investigator must decide on the amount of error that he can tolerate and substitute this in place of $\bar{x} - \mu$, and he must decide on the degree of confidence he wishes and look up the corresponding value of t in the tables given in most textbooks of statistics. It may be useful to remember that when the sample equals 60, t equals exactly 2.000, and that as n increases beyond 60, t changes so little that in empirical work the value of t can be safely called just 2. To illustrate concerning the allowable amount of error, one might expect, for example, that $\bar{x}$ would be about 20; but that an error of 15%, or 3 (i.e., 15% of 20), would be tolerated. Thus, 3 would be inserted in the denominator of the equation for sample size, and it would be squared to become 9.

To use this equation properly, the investigator must have some *prior* knowledge of the variance to be expected. If this prior knowledge were already at hand, the normal procedure would be to then (a) while in the office, estimate the size of sample that is required for the definitive study, and (b) go in the field and collect this sample. Where is one going to get a prior knowledge of the expected variance? It must either come from previous attempts to sample this same population, by essentially the same methods that are now used, or one must make a special pilot study to get the estimate of s^2. That is, if necessary, the worker takes a smallish preliminary sample of the population in the regular way and calculates its variance; the resulting value is then inserted in the equation just given to estimate how big the subsequent main sample must be. Note that one cannot take a sample of the population and then, *a posteriori,* say that the sample was big enough. All one can do is to say that future samples — if taken the same way — will have to be equal to, or greater than, some calculated number in order to give the required precision with the required level of confidence.

What should the investiatgor do to get random samples? First, he usually should *on paper* divide the study area into numerous equal-sized plots. If fairly large areas are involved, the most convenient way to do this is to take an aerial photograph of the study area enlarged to perhaps 10-15 centimeters of photograph per linear kilometer on the ground and to lay out on the photograph a grid of lines that is so constructed as to give the desired number of plots, and then one should give each plot a permanent identifying file number. Finally, the plots to be studied should be selected by drawing their file number from a table of random numbers, such as the table given by Fisher and Yates (1957:126-31) and many authors in textbooks of statistics. This process will tend to rule out human choice of plots to be sampled, and it is usually the most practical way to obtain a random sample on land. Therefore, in terrestrial ecosystems the first of the major assumptions mentioned above can be met, although sometimes, just by chance, and with a probability he can calculate, the investigator will get a "bad sample," in the sense that it will not be very representative of the whole study area. Random sampling in aquatic ecosystems is much more difficult since the space sampled is a volume and boundaries are difficult to establish, a matter which will be commented on further below.

The second major assumption included the idea that all of the animals present on the study plots were counted, but this will almost never be possible unless one is working with large plants, or elephants, or other very large and visible animals. Little need be said on this point, for the most convincing arguments are furnished by each reader's own field work. No matter how carefully the plots are searched, some of the animals are likely to be missed unless the plots are very tiny and searched diligently. There seems to be no practical way to estimate the amount of error caused by not finding all of the animals except to do the "total" counts repeatedly and calculate "efficiency" by the method of Seierstad *et al.* (1967), or to compare results to those obtained from a completely different model.

The highest number seen would, of course, usually be considered the best number, but it could be inflated by chance influx of animals on to the plots from peripheral areas.

Included in the second assumption was the idea that very few or none of the animals were counted more than once, but this may not be true in practice. The assumption is most likely to be met in animals of low mobility, especially when the animals make no particular effort to avoid the observer, as in insect larvae, snails, etc. On the other hand, when dealing with highly mobile animals, such as most adult butterfles and many other arthropods and vertebrates and some members of other classes — some counted animals may move rapidly away from the observer and end up on another plot where they will probably be counted again. However, it is much more likely that, if an animal is unusually mobile, it will flee from the plot before the observer counts him; and is is not likely to be counted later. Thus, in work on highly elusive animals, the method of "total" counts on sample plots frequently gives under-estimates.

In summary, the three major assumptions are difficult to meet, and, hence, "total counts" on sample plots often yield only poor estimates of population desnsity. Although randomness of samples can be attained, the plot size and the sample-size must be increased as clumping increases. Some animals are usually overlooked and not counted, even when searching for them is thorough and careful, but this error may be partially counteracted by the fact that other animals were counted twice or more. Where animals are comparatively wild and mobile, as among many of the insects and vertebrates, the estimates will often be biased downward. Nevertheless, the procedure is

widely used and in many cases is the most practical method of sampling.

In the past, investigators have had no good way to establish whether or not important sampling error occurred when making "total" counts on sample plots, except to estimate population density with several different models and sources of data to see if results approximately agreed. Very recently, however, Seierstad, Seierstad, and Mysterud (1967) gave two procedures for estimating the efficiency of surveys designed to yield total counts. The first of their two methods requires that repeated counts be made on the sample areas, and evidently during each of these the observers attempt to find all of the animals. Due to random events, the total number of animals seen during each complete survey tends to vary somewhat. Seierstad *et al.* assumed that X_i individuals are seen in each total survey (for all sample plots combined) and, furthermore, that the X_i's are independently and binomially distributed. They found that the estimated probability of seeing one specific animal, $\hat{p}$, was given by

$$\hat{p} = 1 - \frac{s^2}{\bar{x}}.$$

After $\hat{p}$ was found, one could of course estimate the total abundance on the sample area from the ratio $x / \hat{p}$. A formula for the estimated variance of $\hat{p}$ was included.

Further details of this procedure of Seierstad *et al.* (1967) will not be mentioned because it seems to result in the same estimator that was derived independently by Hanson and Chapman (in press). The latter workers, however, designed their own method as a primary estimator of population density in its own right when rapid, incomplete counts were to be made, not to determine survey efficiency of total counts. Near the end of the present report the procedure of Hanson and Chapman will be described briefly. The method of Seierstad *et al.* mentioned above and their other one are valuable attempts to give checks on the efficiency of so-called total counts. However, their report did not mention experimental tests of the method and it did not comment on the fact that data from individual animals are seldom distributed binomially.

Before leaving the matter of total counts on sample plots, a peculiarity should be noted; the method normally presumes to apply to areas, whereas animals such as insects, birds, and fishes usually move about in volumes. For example, if the in-

vestigator were studying the question of how many insects of some tree-inhabiting species lived on each "unit area" of a forested tract, he would probably take a volumetric measurement by estimating the number in insects per tree (or per part of a tree) and multiply by the number of trees per unit area. This presents no difficulty in theory except that such estimates do not fit the usual definitions of density and cannot be readily compared to those that do pertain essentially to two-dimensional space. Partly because of this difficulty and also because it is hard to delimit the boundaries of sample plots in aquatic habitats, fishery workers and some other kinds of specialists have emphasized the marking procedures for estimating population abundance or density or both, the subject of the next section.

ESTIMATING POPULATION DENSITY BY MARKING

Introduction

Probably more has been written about estimating density in this way than by all others combined. Chapman (1948) and Schaefer (1951) found that the procedure dates back at least to La Place in 1783, who used the method, in effect, to estimate the human population of France; but Petersen (1896), working in Denmark on fish, is often said to be the first to estimate the abundance of nonhumans in this way. Bailey (1952) and LeCren (1965) believe, however, that Petersen did not use marking to estimate density although he used it for other purposes. Rather, according to LeCren, Dahl (1917) in his book on trout was the first to publish the use of the method on animals. His procedure was explained again in a condensed English translation (Dahl, 1919). Thus, it is not justified to call such marking methods the "Lincoln Index," since Lincoln (1930) did not publish on the matter until later. In the period since 1930, many writings dealing with elaborations of the basic model have appeared, and equations for confidence limits have been derived. The best overall summary and interpretation of the extensive literature so far is that of Ricker (1958). There is much of value on this and many other aspects of population dynamics in the important book by Beverton and Holt (1957). Southwood (1966:57-98) gave a highly useful discussion of the method of estimation based on marking, and he reviewed and cited much literature on the subject.

As is becoming widely known, the underlying idea of the marking methods is that some animals of a population will be

caught, marked alive, and released back into the general population. After the marked animals distribute themselves around to become mixed up with unmarked ones, a new sample is captured, and the fraction of this second sample containing marked animals is determined. Knowing the total number marked, and the effect this total of marked animals had on a later sample — by causing a certain fraction of the sample to bear marks — the investigator can quickly perform the simple arithmetic required to estimate the abundance of the whole group studied.

Although it is most usual to mark the animals artificially, the theory of the method is equally applicable to animals which bear natural marks. Likewise, although it is most usual to recapture the animals, re-observation of free-ranging, noncaptive animals is also adequate if the artificial or natural marks can be distinguished during the second period of sampling.

As usual, valid data must be obtained, and often that is very difficult. Ricker (1958:86) listed several conditions that must be met in order to justify the use of the most basic model on fish populations. These conditions would apply to other populations as well and they are:

1. Marking does not increase natural mortality.
2. Marked animals are neither more nor less vulnerable to the recapturing operations than are unmarked ones.
3. The marks do not come off the animal or otherwise become invisible (as in the case of dyes which fade out), and they are recognized and reported.
4. Either the marked animals mix up randomly with the unmarked ones, or, at least, the second sampling and recapturing is at random with respect to the locations of the animals as a whole.
5. There is little, if any, recruitment to the population.

To Ricker's list here, one can add a further well-known restriction, that

6. Marked animals do not leave the area of study and do not, in effect, become replaced by unmarked ones which move in.

It should be noted that the fifth and sixth requirements above lead to one basic condition, that the fraction of the population bearing marks does not change. Procedures to follow when this fraction does change become somewhat "involved" but are well covered by Ricker (1958:111-144) and others. Steps that might be taken to offset lack of fulfillment of the other conditions were also discussed at length by Ricker (1958:86-100). Obviously

the shorter the time between the two samplings the less the possible effect of recruitment or movement of marked animals out of the area.

Two Samples Taken

The original Dahl (or Petersen) Estimator required two samples only; after the samples were taken a proportion was established that said basically the following:

$$\frac{\text{Number of Animals in Whole Population}}{\text{Number of Animals in First Sample, All of Which Are Marked.}} = \frac{\text{Number of Animals in Second Sample}}{\text{Number of Animals in Second Sample That Had Marks.}}.$$

The equation can be solved for the number of animals in the whole population, but the solution is slightly biased and $\hat{K}$, the estimated total population or segment being studied, diverges more and more from K, the actual total population or total of a segment, as the sample becomes smaller. Several workers have, therefore, proposed helpful refinements of the basic equation indicated above in words, of which one by Bailey (1951) is

$$\hat{K} = \frac{X_1 (X_2 + 1)}{X_{1,2} + 1}.$$

X_1 is the total number of animals in the first sample and all are marked after their capture, X_2 is the total number in the second sample, and $X_{1,2}$ is the number among the second sample that bear marks. The latter symbol carries the subscripts "1,2" to indicate also that these animals bearing marks have to be ones which were caught twice, that is, in sample 1 and sample 2.

The addition of 1 to X_2 in the numerator and of 1 to $X_{1,2}$ in the denominator, Bailey's refinement, has important consequences in small samples, where usually $X_{1,2}$ is especially small, but in large samples the corrected equation of Bailey gives results nearly the same as in Dahl's original expression.

The investigator should, as usual, calculate the variance of $\hat{K}$ so that he can find the confidence limits of his estimate of abundance. Although better methods of calculating the variance have been found (see the review of Ricker, 1958:84-85), it is usually adequate to approximate the confidence limits by reading directly from tables of limits for the binomial distribution, especially if an appreciable fraction of the population is marked, say 8-10% or more.

When looking at tables or charts giving the binomial confidence limits, what is the random event which is initially being studied? The random event is the question of whether or not any given captured animal in the second sample bears a mark; each animal is marked or is not, and finally after looking at all the animals in the second sample, the investigator can establish an estimate of the probability, $\hat{p}$, that any given animal in the whole population is marked. From an appropriate table, such as Snedecor's (1956:4-5), one looks up the confidence limits for the probability that was calculated from the sample. Suppose that a second sample of some particular size had 0.2 marked animals and that the binomial table (for the particular sample size and selected level of confidence) showed its confidence limits to be $\pm$ 0.05. Therefore, $\hat{p}$ was expected to vary from 0.15 to 0.25. As a result, $X_{1,2}$ in the Dahl Estimator would vary up or down accordingly. As one might suspect, the investigator solves the equation for $\hat{K}$ twice, using first the lower limit for $\hat{p}$ and then the upper limit. Some people prefer to use the Clopper-Pearson charts where the confidence belts are shown in graphic form for various sample sizes. Adams (1951) reproduced several of the charts for the binomial confidence limits, as well as several for the Poisson limits, and gave a good discussion of their use. The Clopper-Pearson charts of the binomial limits are also shown in some textbooks of statistics, such as the one by Steel and Torrie (1960:458-459).

To take another example, suppose one found from two samples, involving marking and later recapturing, that X_1 equalled 100 and X_2 also equalled 100, but $X_{1,2}$ equalled 20. Therefore, $\hat{p}$ (the estimated probability that any given animal in the whole population would bear a mark) in turn equalled 20/100. Thus, for some selected level of confidence, say the 95% level, $X_{1,2}$ would be within these limits (Snedecor, 1956:4-5):

$$13 < X_{1,2} < 29$$

Finally, although the best estimate of K would be

$$\hat{K} = \frac{100\ (100 + 1)}{20 + 1} = \frac{10{,}100}{21} = 481.0\ ,$$

$\hat{K}$ could actually vary from

$$\hat{K} = \frac{100\ (100 + 1)}{13 + 1} = \frac{10{,}100}{14} = 721.4$$

down to

$$\hat{K} = \frac{100\ (100 + 1)}{29 + 1} = \frac{10{,}100}{30} = 336.7\ .$$

Multiple Samples Taken (Schnabel's Procedure)

For some time, the original attempts to estimate population density by marking involved just two samples, but subsequently the methods of LaPlace and Dahl were extended to cover numerous samples taken over a longer or shorter period of time and in many different circumstances. As a result, a voluminous literature has arisen on the subject, and has been augmented practically every month to the present time. To date, the best general review of the multiple sampling procedures was given by Ricker (1958:100-144), and his work should be consulted for further details. The papers by Chapman (1952, 1954) and Schaefer (1951) are also of unusual value in this regard.

The assumptions required now are the same as those for only two samples. Multiple marking and sampling can still yield estimates of population abundance even when recruitment or immigration causes change in the fraction of the population marked, but the details of the adjustments which must be made are beyond the scope of the present paper; the interested reader is referred again to Ricker. According to Ricker (1958:100), beginning in the 1930's several workers were known to have used repeated marking and recapture or reobservation, that is, multiple samples; but apparently the first of these to publish the theory of the method was Schnabel (1938). It turned out that her procedure was only a slight, although important, extension of Dahl's (1917) formulation and was as follows:

$$\hat{K} = \frac{\Sigma\left(X_i \cdot X_m\right)}{\Sigma X_{i,m}}$$

As before, $\hat{K}$ is the estimate of total population, but the remaining symbols have been modified slightly; X_i are the animals captured on the ith occasion, that is, on any given occasion one wishes to consider; X_m is the total number of animals that have been previously marked and released alive, that is, those marked successfully in the samples X_1, X_2, ... X_{i-1}; and $X_{i,m}$ is the number of animals in the (i^{th}) sample which bears marks.

As was true of LaPlace's and Dahl's original procedure, the above expression was discovered by biometricians to be slightly biased, the more so as the number of recaptures became smaller. Therefore, for large populations several corrections were proposed, of which Chapman's (1952) adds 1 in the denominator.

Although the adding of 1 in the denominator of Schnabel's original expression may seem like only a slight change, it leads to relatively large differences in estimates of the total population, $\hat{K}$; especially when the sum of the number of recaptures, $\sum X_{i,m}$ is less than, say, 50 or 60.

It must be remembered that, in the multiple capture procedure, the number of captures on each given date, X_i, must be multiplied by the number of animals marked prior to that date, X_m. Then each of the resulting products must be summed cumulatively down through the last date when a sample was captured.

Let us consider the following example: Suppose that 50 mice were caught, marked and released on a given date, the first of a series of samples; on the second date, 40 mice were caught of which 11 were already marked; and on the fourth date, 60 were caught of which 20 already bore marks; following this, the work was stopped. Of course, on the first three dates, any animals not bearing marks when first noticed in the traps were immediately marked before they were released. A table of the data and some resulting computations would look as follows:

Sample Number				
1	0	50	0	0
2	50	40	2,000	8
3	82	35	2,870	11
4	106	60	66,360	20
Σ —	—	—	71,230	39

Therefore, the Schnabel estimate (with Chapman's modification) for the total population was

$$\hat{K} = \frac{71{,}230}{39 + 1} \doteqdot 1{,}781 .$$

Schumacher and Eschmayer (1943), Chapman (1948, 1954), and DeLury (1958) gave formulas for the variance, and Ricker (1958:102-103) has nicely illustrated the use of some of them. However, calculating the confidence limits for the Schnabel-type estimates of population density, by formula, is somewhat tedious and so will not be discussed here.

Fortunately, Chapman (1948) has provided a table that approximates the confidence limits where the ratio of marked to unmarked animals is small and the distribution of marked animals can thus be approximated from the Poisson distribution.

Within the body of Chapman's table, reproduced here as Table 1, he gave the upper and lower bounds, at the 95% confidence level for the ratio $K/\Sigma(X_i X_m)$; and he has set these bounds opposite to appropriate values of $X_{i,m}$. We notice that since Chapman's table shows the confidence limits for the ratio $K/\Sigma(X_i X_m)$, it is easy to "plug in" ones own observed values by multiplying the product $(X_i X_m)$, from the last line of the data in a Schnabel table, times the lower bound which was read off from Chapman's table. This is equivalent to cancelling the denominator of $K/\Sigma(X_i X_m)$ and leaves just K, or that is in this case the estimated smallest total number of animals on the study area. The same procedure would be repeated for the upper bound shown in the table, and it would give the upper bound for K.

In the hypothetical example shown above, the last line of the Schnabel-type table gave a sum of 39 animals which were found to bear marks when recapturing was done. Therefore, one would enter Chapman's table, Table 1 of this report, where $X_{i,m} = 39$, for which the ratio $K/\Sigma(X_i X_m)$ has limits of .01805 and .035. Multiplying the latter two fractions times the sum of $(X_i X_m)$ shown in the last line of the example, that is, 71,230, one gets about 1,282 and 2,493; these are, therefore, the upper and lower limits at the 95% confidence level for the number of mice that was estimated in the example above to be 1,781.

As the sum of the recaptures increases, the confidence limits narrow rapidly because the Poisson distribution is less skewed as sample size increases. Although, as can be seen, the original table extended only to a total of 50 recaptures, large-sample theory based on the z-distribution could be used for totals larger than 50, as Chapman (1948) pointed out. That distribution would provide an approximation to the binomial distribution, where the fraction of the total captures that bore marks is considered the mean of the binomial events, but the interested reader should consult statistics textbooks for a review of this.

Many other developments based on marking have occurred. In fact, Ricker (1958:81-83) showed that four major methods and two or three variations of each are available for estimating population density by marking. "Point" sampling, or "Jackson's method" is a major variation that will now be mentioned briefly.

During the preceding discussion, it was implicitly understood that the population was closed, that birth, or death, or migration, or some combination of them did not occur in the time between samplings; or, if one or more did occur, they did not change the

TABLE I.

95 Per Cent Confidence Limits for $K/X_i X_m$

X_{im}	*Lower Limit*	*Upper Limit*	X_{im}	*Lower Limit*	*Upper Limit*
0	0.0885	.....			
1	0.0720	19.489	26	0.02478	0.0563
2	0.0767	2.821	27	0.02408	0.0539
3	0.0736	1.230	28	0.02342	0.0516
4	0.0690	0.738	29	0.02279	0.0495
5	0.0644	0.513	30	0.02221	0.0475
6	0.0600	0.388	31	0.02165	0.0457
7	0.0561	0.309	32	0.02112	0.0440
8	0.0526	0.256	33	0.02061	0.0425
9	0.0495	0.217	34	0.02014	0.0410
10	0.0468	0.188	35	0.01968	0.0396
11	0.0443	0.165	36	0.01925	0.0384
12	0.0420	0.147	37	0.01883	0.0372
13	0.0400	0.133	38	0.01843	0.0360
14	0.0382	0.121	39	0.01805	0.0350
15	0.0365	0.111	40	0.01769	0.03396
16	0.0350	0.1020	41	0.01733	0.03300
17	0.03362	0.0945	42	0.01700	0.03210
18	0.03233	0.0880	43	0.01668	0.03124
19	0.03114	0.0823	44	0.01636	0.03043
20	0.03004	0.0773	45	0.01606	0.02966
21	0.02901	0.0729	46	0.01578	0.02892
22	0.02806	0.0689	47	0.01550	0.02822
23	0.02716	0.0653	48	0.01523	0.02755
24	0.02632	0.0620	49	0.01498	0.02691
25	0.02552	0.0591	50	0.01475	0.02625

I am grateful to Dr. Chapman for permission to reprint this table.

tag ratio (of marked to unmarked animals.) However, the "point" sampling method contains refinements that can be used to estimate density even when extraneous changes do occur, and also the method permits estimates of birth and survival rates. The general approach seems to have been originated mainly by Jackson (1936; 1939) while analyzing a population of tsetse-fly (*Glossina morsitans*). However, the work was immediately, or perhaps concurrently, expanded in the "trellis diagram approach" by Dowdeswell, Fisher and Ford (1940), because the latter authors state (p. 131) that, "The theory of the interpretation of recapture frequencies has been gradually developed in collaboration with Dr. C. H. N. Jackson for many years during his researches on the tsetse fly in Tanganyika territory," and, moreover, Jackson in his 1939 paper (p. 246) acknowledges the "invaluable help" of Prof. R. A. Fisher and Mr. W. L. Stevens.

Two main variations were published by Jackson: In the first, called the "positive method," one short period of marking is done, but a number of periods of recapture take place; in the "negative" method, marking is done on a number of dates but recaptures are made on one date. Andrewartha (1961:26-34) discussed the method, including the trellis diagram and illustrated with detailed examples (pp. 202-210). The explanation of the "point" sampling method of estimating population density, given by Jackson (1939) himself, is fairly clear, and the brief treatment in Dowdeswell, Fisher, and Ford (1940) is commendable. Numerous others have studied the method and their contributions are evaluated by Chapman (1954).

In the present relatively brief review of a huge field, it is intended only to indicate some of the main developments, and therefore, the equations for the "point" sampling techniques will not be mentioned, particularly since the procedure necessarily becomes somewhat "messy" and involved. However, the following may indicate a general line, without regard to any specific publication, that can be followed to go around the problem of deaths, births, and other factors which change the tag ratio.

As is well known, one can estimate mortality and survival rates in a stationary population by (a) marking a cohort of animals in a very brief period, (b) capturing successive samples at later times in the future, in order to study change in the tag ratio as the marked animals die out and are replaced by

unmarked ones, and (c) calculating the rate of mortality in these marked animals from the change in tag ratio. (This or something similar is commonly done in constructing an age-specific life table, for example.) Knowing the rate of decline in the marked component and its rate of replacement by unmarked animals, one can then calculate how many marked animals should have existed on some prior date if a given number exists now. This same idea of projecting backward can be used when the decline in marked animals is due to egress from the area, or when it is due to a combination of death and egress. Thus a corrected number of recaptures can be derived and the total abundance estimated, all in spite of the fact that the tag ratio was changing as sampling continued over a fairly long period of time.

In brief summary, the marking methods are extremely valuable and consequently widely used. Fortunately, the estimators do not require the data to form any specific distribution, although the confidence limits for the models require specific distributions of data. The biological problems are, as usual, more acute than the statistical ones, and eventually they tend in many cases to violate the assumptions on which the models rest, especially when multiple sampling is used and longer periods of time go by. Changes in the animals' behavior cannot readily be compensated for by statistical refinements, and herein lies the principal shortcoming of the marking methods, the tendency for the animals to become trap-prone, net-shy, etc. Moreover, many man-hours of work and much expensive trapping material are often required to catch and mark the animals, especially among the keen, mobile ones such as the mammals and birds. If a net can be used to strain the animals out of an aquatic or gaseous medium, or better yet, if the animals can be attracted to a light as in the case of many insects, the cost of the marking methods can be much reduced. Regardless of the problems, the investigator will often be well advised to estimate the density of his specific populations by several methods, including this one, to determine the amount of agreement among the estimates.

ESTIMATING POPULATION DENSITY BY THE REMOVAL METHOD

Introduction

"Removal methods" of estimating density are evidently much newer than those based on marking, because, according to Davis (1963:103), they were first used in 1914 in Norway on bears by Hjort and Ottestad (see Hjort *et al.*, 1933). Leslie and Davis (1939) also published the method, theirs being the first well known report on this procedure. According to a valuable discussion by Ricker (1958:145), a number of other workers published reports on the technique in several countries as early as the 1940's, but not until DeLury (1947) refined the procedure did it come into common use in fiishery ecology. Moran (1951) derived maximum liklihood equations for estimating density by the removal method, but his procedure is a special case of DeLury's (1947) more general method, according to Zippin (1956). Methods for finding the confidence limits were presented by DeLury (1951), Chapman (1955), Zippin (1956, 1958) and others.

During each year additional publications on the removal method are appearing, and already the literature on the subject is growing heavy although it has some way to go to equal the work on the marking procedures. Fortunately, the report of Hayne (1949a) and the reviews by Davis (1963:103-117), Ricker (1958:145-184), and Chapman (1954, 1955) are excellent, and they should be consulted for details. The reports by Zippin (1956, 1958) also give syntheses valuable for both biometrists and practicing ecologists. Southwood (1966:174-186) briefly reviewed removal methods, including how the data might be obtained among insect populations. Recently, Rupp (1966) has simplified the field by showing that the removal methods and tagging methods are, in principle, special cases of one and the same scheme.

The underlying theory of all the removal methods for estimating population density is that removing a known number of animals will cause a measurable change in some quantity that can be determined by sampling. Some of the principal variations on this theme are: (1) number of removals on each given date (per unit of effort, i.e., per day, per trap-night, etc.) compared to total previous removals, (2) comparison of number of re-

movals (per unit of effort) on successive dates, (3) the amount of change in the observed sex or age ratio caused by a known amount of removal, or (4) the amount of change in the number of one species compared to another caused by a known amount of removal, etc. Many other possible ratios can be studied from the standpoint of their change resulting from a known amount of captures (and removals).

The first two general methods are closely similar to each other and the only applicable difference is whether the periodic catch shall be summed cumulatively or considered separately in the individual samples. The third method, involving change in sex or age ratios, at first thought appears much different, but, as was brought out by several writers (for example, Davis, 1963:106), the general idea is closely similar to the other removal procedures; the principal point of departure is that the animals need not be captured to obtain ratios if the various sex, or age, or other components can be distinguished in the field and the animals are removed only once.

Other developments included Hayne's (1949a) proposal that the periodical catch be plotted on the Y-axis against the cumulative catch on the X-axis and the results be analyzed by regression methods; the point where the curve intercepted the X-axis would indicate the estimated total population. In addition, DeLury (1951) made the valuable suggestion that the removal method and the marking method should be used at the same time; animals should be trapped alive, marked, released, and some would be captured again, but any that bore marks would be considered "dead" mathematically. Thus, successive captures would have fewer and fewer unmarked animals due to the mathematical (but not real) removal of marked ones. Chapman (1955) also considered the combination of tagging and removal work in one study.

Assumptions and Data

The usual assumptions on which the removal methods rest were covered by, among others, Ricker (1958:151-152), Davis (1963:105), Zippin (1956), and Chapman (1955); and Zippin condensed them down to three main ones:

1. The population must be essentially stationary during the period studied, except for the change caused by the investigator's removal; that is, births, deaths, immigration, and emigration do not occur, or at least, their effects cancel

out. However, Lander (1962) and Chapman and Murphy (1965) have shown that these problems are much lessened when one is estimating density with what the latter call "survey-removal" methods, i.e., those involving removal with associated change in sex or age ratios, etc.

2. The probability of capture (or removal) is the same for each animal.
3. The probability of capture (or removal) for any given animal is the same during each different period when capturing (or removing) is done.

To these I would add:

4. In all but the survey-removal methods, the unit of effort during successive removals must be approximately constant.

As the authors mentioned above and other workers pointed out, the assumptions are frequently not fulfilled, especially when the removal is carried out over a long period of time. The longer the period of time that has elapsed, the more that animals from outside of the area of study are likely to move in and take over the home ranges of animals that man has removed; the mathematical removal of live (tagged) animals that are returned to the population tends, however, to overcame the problem of ingress, inasmuch as the animals' home ranges obviously do not become vacant when the animals are returned alive to the general population. Also, the longer the time between surveys, the more likely that the population abundance will change due to births and deaths, and the more likely that the behavior of the animals will also change.

A pecularly bad problem with removal methods is the change in "catchability" of the animals, since, of course, those animals that are most accessible, most favorably inclined toward the trap bait, least wary, etc., will tend to be removed first; and the longer that the netting, trapping, fishing, or shooting goes on, the more difficult it will be to capture the average animal still remaining at large.

The amount of effort expended by the investigator during successive removals is probably often not the same. Even though the trapper (netter, hunter, etc.) may put in the same number of hours on each period or removal, he may work harder during some than during others, or his work may gradually become more efficient as he continues, resulting in higher catches of animals in relation to the number then present. In the survey-removal variation, usually only one removal is made, and of course then variations in effort or variations in probability of

capture are not harmful.

Inconstant susceptibility of the animals to the capturing technique is the largest potential source of error, according to Ricker (1958:151), for most of the removal techniques. As usual, we should estimate population density by a variety of methods and compare the results to better judge the reliability of the several estimates.

To sum up the bases on which removal procedures rest, one finds that two main comparisons may be made among the "removed" elements: (a) current removal from the population at large as compared to previous removals, or (b) removal of some restricted natural segment of the population, such as a sex or age class, compared to removal of some other class. Concerning removal among the population at large one may have (1) actual removal or (2) marking and replacement of live animals that are treated mathematically as dead. The resulting estimates of the population will obviously be made by either (a) plotting the data on graph paper and drawing the best linear regression line obtainable from gross visual inspection or, preferably, from fitting the line by the least squares method; or (b) by solving various formulas, collectively called "multinomial methods." From the standpoint of analysis, actual removal and mathematical removal of animals drawn from all of the components ofthe population can be handled by the same models, whereas the techniques requiring a selective removal of some restricted component of the population (as a sex or age group) require somewhat different approaches, especially inasmuch as only one removal normally occurs in practical work.

Current Removal Relative to Previous Removal

Regression — The number of animals removed on a given date per unit of effort, or per cumulative total of animals previously taken, etc., yields one point on a graph. When the same work is extended over several dates, successive points in a scatter diagram can be drawn. It is straightforward and relatively simple, to calculate the line of best fit, based on the well-known least-squares regression. The formulas for linear regression are given in textbooks of statistics. Let it be supposed that one plots the number of animals successively removed (either actually or mathematically) per unit of effort against the total number of animals previously removed. Let it be understood that the number caught per unit of time, such as per trap night, will be the dependent variable Y and the total number of animals previously caught will be the independent variable X. (The "unit of effort"

must be closely controlled or large errors will result.) Then, in the standard terminology of regression methods (see for example, Snedecor, (1956:123-125),

$$\hat{Y} = b(X - \bar{x}) + \bar{y},$$

where $\hat{Y}$ is the best-estimated value of Y as defined above; $\bar{y}$ is the average of the Y's, that is, the average number of animals captured per unit of time; $\bar{x}$ is the average of the X's, that is, the average of the cumulative total number of animals captured during the entire period. Regarding the latter, consider, for example, that 25 animals were trapped the first night, 21 the second night, 18 on the third, and 12 on the fourth. The cumulative totals are, respectively 25, 46, 64, and 76, for which the average, x, would be 53. To continue, with the symbols, the symbol b is defined by

$$b = \Sigma xy / \Sigma x^2,$$

where x is the deviation of X from $\bar{x}$ and y is the deviation *of* Y from $\bar{y}$. b is called the regression coefficient; it gives the slope of the regression line, because for every change of 1 unit in X, there will be a change of b units in Y. Thus, the line of best fit can be calculated and drawn; where is crosses the abscissa will be the estimated total population of the area sampled. In addition, and this is rather important, confidence limits for the fitted regression line can be rather easily found from the equations given in the many books of statistics.

Multinomial Methods — When the animals are removed from the population at large, either actually or mathematically, and this is done only twice, the population density may be estimated from the simple relationship (Zippin, 1958) :

$$\hat{K} = \frac{Y^2_1}{Y_1 - Y_2}.$$

As usual, $\hat{K}$ means the estimated total number of animals present, Y_1 is the number removed during the first period of capture, and Y_2 is the number removed during the second period of capture. If the animals are removed during exactly three, four, five, or seven periods, the total size of the population may be rapidly calculated with the aid of charts, given by Zippin (1956, 1958), based on maximum likelihood equations.

In actual practice, the investigator would seldom use more than seven periods of removal, because by then the remaining (nonremoved) population would have become so small that additional efforts would tend to be unproductive and also because enough data would already have been obtained. However,

if one still wants to conduct more than seven periods of removal, the maximum likelihood equations provided by Zippin (1956, 1958), based on Moran (1951), can be used. As can be seen from Zippin (1958), the following "nasty" expression must be solved for $1 - q$, the probability of capture:

$$\frac{(1-1)\,y_1 + (2-1)y_2 + \dots (n-1)y}{y_1 + y_2 + \dots y} = \frac{\hat{q}}{1-\hat{q}} - \frac{n\,\hat{q}^n}{1-\hat{q}^n}.$$

Here y_1 is the number of animals removed on the first occasion, y_2 is the number removed on the second occasion, etc. up through the nth period or removal; and $\hat{q}$ is the estimated probability that an animal will not be captured (and removed). $1 - \hat{q}^n$ gives the probability that an animal will be captured after n attempts (since $p = 1 - q$). Finally, the estimated total population $\hat{K}$ equals the total catch $\sum_{i=1}^{n} y_i$ over the probability of capture, thus:

$$\hat{K} = \frac{\sum_{i=1}^{n} y_i}{1-\hat{q}^n}.$$

The question comes up, when using the removal method, is it better to estimate population density by plotting the data and calculating the regression or is it better to use Zippin's charts and/or multinomial equations. Zippin (1956, 1958) analyzed this question rather thoroughly, and he concluded (1958) "a least-squares regression gives estimates that are as good as multinomial estimates; however, this method requires considerably more time to calculate than the multinomial estimate made using the graphs. The regression method may be recommended when the graphs are not available."

In my judgement, if more than two periods of capture are used, the best all-around procedure for most workers will be to calculate the regression from the well-known equations because (a) most workers are already familiar with the technique of calculating regression lines; (b) most workers have access to desk calculators, and consequently the time needed to perform the arithmetic is negligible, especially in relation to the time required to obtain the data; and (c) it is easier to calculate the confidence limits of a regression line by the familiar methods than it is to calculate the limits from the maximum liklihood equations of Zippin (1956).

Survey-Removal Procedures

Removal methods that involve unequal capture of two or more segments of the population and thereby cause a change in sex, or age, or other ratios have proliferated in recent years, although the procedure seems to trace back to the important papers of Kelker (1940, 1944). The statistical theory underlying the field has been developed by Chapman (1955) and Chapman and Murphy (1965), and other aspects were reviewed by Hanson (1963).

Among the many survey-removal procedures, one will now be briefly described to illustrate the general field. This one compared unequal numbers of males and females, but the theory can be extended to many other situations (Davis, 1963:106). Two randomized field surveys are made, one before the period of removal and one afterward, and the surveys yield the sex ratio of the animals during the pre- and post-removal times. Next, one must obtain a total count, i.e., a census, of all removed animals of each sex, or age group, or other components being compared.

Kelker (1940, 1944), Rasmussen and Doman (1943), and Petrides (1949) have published valuable survey-removal procedures for analyzing the situation where two segments of the population are removed, all of which were compared by Hanson (1963:53-58). However, since the method of Petrides (1949) seems a little easier to understand, it will be reproduced here, as follows. It is assumed that the ratio studied does not change except due to man's removal. Two proportions are established, as follows:

$$(1)\quad \frac{\text{Total Number of Mature Males, in } \textit{Pre}\text{removal Population} - \text{Total Number of Mature Males Removed}}{\text{Total Number of Mature Females, in } \textit{Pre}\text{removal Population} - \text{Total Number of Mature Females Removed}} = \frac{\text{Relative Number of Mature Males in } \textit{Post}\text{removal Sample}}{\text{Relative Number of Mature Females in } \textit{Post}\text{removal Sample}}$$

$$(2)\quad \frac{\text{Total Number of Mature Males, in } \textit{Pre}\text{removal Population}}{\text{Total Number of Mature Females in } \textit{Pre}\text{removal Population}} = \frac{\text{Fraction of a } \textit{Pre}\text{removal Sample Composed of Mature Males} \times \text{Total Number, of All Sexes, in } \textit{Pre}\text{removal Population}}{\text{Fraction of a } \textit{Pre}\text{removal Sample Composed of Mature Females} \times \text{Total Number, of All Sexes, in } \textit{Pre}\text{removal Population}}$$

The foregoing concepts in the word equations will now be symbolized as follows: A_b, total males in population, before removal; E_b, total females in population, before removal; A_d, toal males removed; E_d, total females removed; M_b, number of males in sample, before removal; F_b, number of females in sample, before removal; M_c, number of males in sample, after (at completion of) removal; F_c, number of females in sample, after removal; U_b, total number of all sexes, in whole population, before removal; and N_b, number of animals of all sexes, in sample, before removal. Therefore, the two basic proportions of Petrides (1949) were

$$\frac{A_b - A_d}{E_b - E_d} = \frac{M_c}{F_c},$$

and

$$\frac{A_b}{E_b} = \frac{\frac{M_b}{N_b} \cdot U_b}{\frac{F_b}{N_b} \cdot U_b}.$$

It is obvious that M_b / N_b gives the fraction of a sample which is composed of males before removal and that F_b / N_b gives a comparable fraction for females. After the two major proportions of Petrides given above are solved simultaneously by the usual methods, they will yield U_b, the total number of the entire population before the removal began. In the process, the worker eliminates from the first proportion the unknowns A_b and E_b by putting into the first equation the equivalent expressions shown on the righthand side of the second equation. The final result gives:

$$U_b = \frac{N_b\,(A_d F_c - E_d M_c)}{M_b F_b - M_c F_b}.$$

Variance When Population Closed. — Formulas for the asymptotic (large-sample) variance of the abundance (estimated from survey-removal methods) were developed by Chapman (1954, 1955). Apparently, many ecologists are not aware of his variance formulas for the survey-removal estimates, perhaps partly because Chapman's two articles were published in journals of theoretical statistics and written in a technical mathematical style. Unfortunately, Hanson (1963) overlooked both of these important papers; and although Davis (1963:103 and 114) cited both of the papers by Chapman, he said (p. 106) in his excellent review that no estimate of variance was available for the "sex ratio method" (survey-removal procedure).

The asymptotic variance of the population's estimated abundance before the removal began, $\sigma^2(\hat{N}_o)$, was given by Chapman (1955) as

$$\sigma^2(\hat{N}_o) = \frac{\dfrac{X_o Y_o}{n_o} + \dfrac{X_1 Y_1}{n_1}}{(P_o - P_1)^2}$$

The symbols used above are those of Chapman and have the following meanings: First, the subscript "O" refers to the beginning of a period of time, that is, to the time when the first of a pair of field surveys is made; the subscript "1" refers to the end of this time period, or the occasion of the second survey, made after the removal was over (and of course the subscript "i" is a general description meaning here "any given time selected"). X_i and Y_i are the size of classes X and Y at times t_i, and the two classes combined make up N_i, the total population at time t_i. P_i is the fraction of the total population made up by a given class; that is, $P_i = X_i / N_i$; and n_i equals the size of the ith sample. X_i and Y_i would have to be replaced by their expectation, the estimates previously derived from the equations of Kelker (1940, 1944) or ones similar to them, such as Petrides' (1949) discussed above, since obviously the true size of any given population component would not usually be known.

Estimates When Population Not Closed. — Most workers using the survey-removal techniques of estimating population density have assumed that the population ratios did not change appreciably in the time between the field surveys except due to man's removal. In other words, either the population was closed or,

if not closed, the extraneous factors were not appreciably changing the ratios investigated. Although most populations, of course, suffer natural mortality, have members moving into and out of the population, and experience other changes, nevertheless it is reasonable to believe that most of these factors do not usually change the ratios enough to cause any large amount of error, particularly if the time between surveys is reasonably short. Certainly, compared to sampling errors, these other potential errors should be small. If the investigator has good reason to believe that his assumption is not being met, he might shift attention to other population parameters; perhaps sex ratios instead of age ratios, for example.

Lander (1962) considered methods for estimating the rate of fishing or other removal by man based on, he said, "knowledge of catch and of the change in composition caused by selective removal of one class during the catch interval." Lander continued, "From a mathematical viewpoint it [the paper of Lander] simply shows how Chapman's (1955) fundamental work relates to the theory of fishing as developed by authors like Ricker (1958) and Beverton and Holt (1957)." Among other things, Lander presented a model which yielded the "fishing rate" even where natural mortality occurred in the time between surveys. He concluded that unequal rates of natural mortality directed at the classes studied "may not be serious in practice," especially when the class whose rate of capture was being estimated also suffered a higher rate of natural mortality than the other class. Lander presented considerable theoretical material but developed the mathematics clearly in easy stages. Although Lander's paper dealt mainly with estimation of capture rates, it contained much of value on estimating population abundance, since, of course, once the rate of capture is estimated, the actual number of animals caught can be divided by the rate to give the estimated abundance.

Chapman and Murphy (1965) gave several models for estimating population density under several different conditions of an open system and gave their variances. Besides deriving the instantaneous rate of fishing or other removal by man, where the instantaneous rate of natural mortality on the X class, M_x, equals that on the Y class, M_y; they also developed the more interesting case where the natural mortality rates of the classes were different. To accomplish the latter, they invoked again the idea of amount of effort spent on the capture. In other words, when the classes had unequal natural mortality, Chapman and

Murphy inserted factors in their models to take account of removal rate per effort expended and combined this with parts of the standard survey-removal theory. After some comparatively elaborate mathematics, they finally obtained an approximation to the instantaneous rate of natural mortality for the case of a continuous removal ("a constant level fishery," etc.). However, Chapman and Murphy concluded that the estimates of the capture rates "are essentially independent" of the natural mortality rates, and "Furthermore, it is reasonable to believe that if M_x and M_y are not too widely different and are small relative to F_x, again a common fisheries situation, the estimate of F_x will not be appreciably affected by the inequality of M_x, M_y." (F_x is the instantaneous rate of removal by man, in the notation of Chapman and Murphy, and M_x and M_y are the instantaneous rates of natural mortality on the X and Y classes, respectively.)

The report by Chapman and Murphy (1965) contained considerable discussion of the assumptions involved in their models and gave variances, and for these and other reasons it is a valuable contribution. Unfortunately, since the equations were developed in a terse mathmatical style, with little discussion or explanation, the report tends to be obscure.

Similarity of Survey-Removal Methods and Marking Methods

Rupp (1966) has pointed out that many methods of population estimation based on the changes in abundance of one class relative to another have an underlying common basis and, in fact, are identical if it is understood that the symbols for the classes which are compared can be positive or negative, depending on whether animals are added to or removed from the population. In the case of marking experiments, the marked animals can be considered, in one sense, a new group that has been added to existing components.

After giving the usual assumptions, Rupp defined symbols similar to the following:

N_i = population size at time i.

1,2 = subscripts showing the beginning and end of period studied ($i = 1,2$).

p_i = decimal fraction of population in a selected class, such as M, at time i.

M, F = actual number of animals added to or removed from a selected class compared to a contrasting class, such as, respectively, males and females.

Furthermore, and this is important, Rupp required that M and F could each take on positive or negative values accordingly as the animals were added to the population or removed. As usual, p_1 had to differ from p_2 as a result of the addition or removal.

Rupp then wrote two basic equations:

$$p_2 N_2 = p_1 N_1 + M,$$

and

$$N_2 = N_1 + M + F.$$

The first equation implies on its left side that the number of the total population, at the end of a period of study, composed of a selected class such as M equals the number that it composed at the beginning plus the number M added (or removed); one must remember that M can be positive or negative and, hence, one may be adding a negative number on the right. The second expression was substituted for N_2 in the first equation, and the result was solved for N_1:

$$N_1 = \frac{M - p_2(M + F)}{p_2 - p_1}.$$

Rupp (1966) showed that the Dahl (1917) equation based on marking is a special case of the above equations where $p_1 = 0$. Let M now be the class bearing marks. Therefore, if $p_1 = 0$, it is implied that when the period of study began, no animals bore marks. Thus, in the initial equation of Rupp, $p_1 N_1 = 0$, and so

$$p_2 N_2 = 0 + M = M.$$

The latter equation can be rewritten as

$$p_2 = M / N,$$

and when R / M is substituted for p_2, it gives finally the old familiar Dahl estimator $M / N_1 = R / M$. (R = the number of animals in the second sample which bear marks, and, hence, are recaptures.)

Rupp's (1966) formulation seems to contain one minor inconsistency (mostly just a matter of definition) where he said that N_1 could be assumed to equal N_2 when his equations above reflect "addition" of marked animals to the population. The difficulty is that the marked animals are treated as though they are actually added to the population, but of course they are ones already present that are simply converted to a marked status. Therefore, in the second of Rupp's two most basic equations, which was

$$N_2 = N_1 + M + F$$

if $N_2 = N_1$, as stated by Rupp, then some number of unmarked animals, that later becomes marked, designated by me as U, must be added to the left side of the equation to balance, where it is understood that $U = M + F$. This would, in a marking experiment, convert the last equation above to

$$N_2 + U = N_1 + M + F;$$

but since $F = 0$, then $U = M$, and the result is, as it should be,

$$N_2 = N_1 + (M - U) + 0$$

or

$$N_2 = N_1 + (0) + 0.$$

The same result seems to be achieved by a somewhat peculiar method in Rupp's equation (4) which is not well explained; perhaps the problem is mainly one of definition of symbols. Rupp (1966) points out that one component such as M could be "added" to the population (by marking) at the same time another component such as F is removed; in that case F would of course not equal 0 in the equations above.

Rupp's interesting report gives the same conclusion that a number of us heard expressed in a class in 1963 by one of the instructors, Dr. W. Scott Overton, now of Oregon State University; and possibly the idea has occurred to others. The report of Rupp bears out Dr. Overton's oral, and Davis's (1963:118) written, statement that many of the methods for estimating population density are essentially the same or closely similar, that in reality the population ecologist has few basic methods available, and that he needs more.

In summary, the removal methods may be considered from mathematical, biological, and economic standpoints, all of which interact to some extent. Simple yet sound removal models are available, and more are being developed. On the other hand, Zippin (1956) found that the precision of estimates based on removal per unit effort was relatively low. For example, if one wanted the coefficient of variation to be not over 20%, a rather low degree of variation for biological work, and if the true population size was 10,000, then 2,500 animals, or 0.25 of the population, were required to be removed. If the population contained only 1,000 animals, 0.45 of them would have to be removed. If the total population was smaller or if a higher degree of precision was required, an even higher fraction of the population would of course need to be removed. Further, as Zippin (1956) remarked, although it is normally assumed that the population is stationary and that the probability of capture is approximately constant, in fact both requirements are fre-

quently not met. However, in my opinion the need for a constant probability of capture can be relaxed a good deal, for if this probability lessens in some regular, systematic way, a suitable regression curve can still be fitted. In general, when numerous periods or removal occur, it is better to calculate the density by regression methods than it is to do it by formula, partly because the regression relation does not have to be linear. When mathematical rather than actual removal is used, the influx of new animals into vacated home ranges is lessened, and it is more economical to combine marking procedures with the removal ones. Survey-removal procedures, involving change in sex or age ratios or other relative numbers, rest on assumptions that can be more easily met than those of the marking category, according to Chapman (1955), but "... in almost all cases the capture-recapture estimation procedure will yield more information for the same amount of effort." In cases where hunters or fishermen carry out the removal the reverse should be true. In many species the survey-removal models of course cannot be used because no obvious sex or age or other distinction between the classs can be readily recognized in the field. The principal difficulty with the survey-removal methods is that the sex or age or other class of the population often exhibit different behavior, leading to unrepresentative samples from the field. If the removal is by shooting, a number of dead animals may be lost in the field, making the count of total removed animals wrong. In spite of these problems, the removal methods should hold much promise and should be investigated more. Menhinick (1963) got better estimates with them than he did with marking or with total counts on sample plots when he studied several kinds of insects. As usual, the worker should estimate density by several methods and compare results.

ESTIMATING DENSITY FROM STATISTICAL DISTRIBUTION OF DATA

Frequency of Capture

A newer group of methods for estimating population density of animals is that based on the frequency with which a recognizable given animal, or group of animals, is seen 1 time, 2 times, 3 times, etc. Of course, in most surveys, some of the animals will be seen 0 times, and the trick of the present class of methods is to estimate the size of this missing category. After the num-

ber of animals seen 0 times is estimated, the number can be combined with those positively known to be seen 1 or more times to give the estimated total. The present group of methods requires the investigator (a) to mark or otherwise positively identify individual animals and make repeated surveys to determine how often identifiable animals have been seen, (b) to decide what is the underlying distribution from which the truncated data are drawn and then (c) to estimate the size of the missing class either from the formula for the distribution or from regression methods. Some of the main variations based on frequency-of-capture involve (a) the type of distribution assumed, whether Poisson, negative binomial, geometric, or a logarithmic series; and involve (b) whether the models are maximum likelihood estimates or are moment estimates.

Craig's (1953) paper is the earliest on the subject seen by me and it was called to my attention by Dr. William Hovanitz. Hovanitz has told me that during his own research on butterflies he independently noticed the possibility of estimating the size of the missing 0 class with use of formulas for the Poisson distribution; he later asked Dr. Sewall Wright's advice on mathematical procedures that should be followed. Wright furnished a model; Hovanitz developed another. Hovanitz made all his data available to Craig who presented six models, of which Method I was due to Wright, Method 2 was Hovanitz's general approach and Method 5 was due to Stevens (1937).

To return from this little historical sidelight, the models derived by others and presented by Craig, and those due to Craig himself, are valuable contributions to the ever-growing literature on population estimation. In addition, to giving the density estimators, Craig (1953) furnished the variances for the six models, and illustrated with data on butterflies furnished by Dr. Hovanitz (and amply credited to him). The animals must be individually identifiable, requiring normally that they be captured, marked, released, recaptured, and so on, through as many cycles as possible. As usual, the captures must be at random. At once it can be seen that the frequency-of-capture techniques should be combined with marking work for the Schnabel equation; and, therefore, the remaining assumptions underlying the Schnabel approach would have to hold.

Craig (1953) concluded that, although the maximum liklihood estimators gave substantially the same results as did the moment estimators in trials on actual field data, "nevertheless with increasing sample size meaningful solutions of the liklihood equations do not exist." Therefore, I shall reproduce here Method 1 (of Wright) and Method 2 (of Hovanitz and Craig), both moment models and both requiring data from a Poisson distribution. Symbols of Craig, slightly modified, to fit the case where only two periods of capture are used, are:

r = total number of different animals captured.

x_i = class size showing number of times an animal was captured ($x = 0, 1, 2...$).

$s = s_1 = \Sigma x_i f_i$ = total number of captures of the r animals = "first power sum".

$s_2 = \Sigma x_i^2 f_i$ = "second power sum".

f_x = number of animals caught x_i times.

n = animals existing in the whole population.

$\hat{n}$ = estimate of n.

1,2 = subscripts designating the number of times a given animal is caught.

Method 1 is the equation:

$$\ln n - \ln (n - r) = s / n ,$$

where ln signifies of course the natural logs. The solution to the equation has to be iterative, by guessing a value of n, inserting it in the equation, and noticing how close the equation is to balancing. If not close enough, a new estimate of n is tried, etc. According to Craig (1953) the above equation can be "readily solved for the integer n which most nearly satisfies it by the use of a good table of natural logarithms," but in my experience the equation is difficult to handle.

Method 2, on the other hand, is simple to solve but gives coarse estimates; if desired, a trial value of n can be quickly found from Method 2 and inserted into the more exact formula for Method 1, as pointed out by Craig (1953). The equation for Method 2 is:

$$\hat{n} = s_1^2 / (s_2 - s_1) .$$

Craig found the variance for "the proportional error of the estimate of n" by Method 2 to be

$$\sigma^2_{\hat{n}/n} = 2n / s_1^2 .$$

Craig showed the following example, based on Hovanitz's data on butterflies (*Colias eurytheme*):

x	f_x
0	—
1	66
2	3
Σ	69 = r; s = 72.

$$\hat{n} = 72^2 / (78 - 72) = 864,$$

$$\sigma^2_{\hat{n}/n} = 2\,(864) / 72^2 = 0.333.$$

That is, the variance was 1/3 of the estimate of n in this example, or very high, because only a small part of the population was sampled in that particular experiment.

Tanton (1965) estimated the population density of a mouse (*Apodemus sylvaticus*) by a frequency-of-capture model, devised by Brass (1958), and based on an underlying negative binomial distribution. As Tanton said, if the "catchability" of the animals had stayed the same throughout the population when the capturing was done, then a Poisson model would have been appropriate, but, since catchability varied, then the negative binomial was more suitable.

According to Tanton, his estimate was obtained directly from Brass's (1958) Method A. Although Brass said that his paper considered "simplified" methods of fitting the truncated negative binomial distribution, nevertheless the manipulation became fairly involved, particularly for estimating the variances. Tanton converted the observed number of animals captured 1, 2,....n times to fitted numbers, derived somewhat laboriously, from which estimates of parameters were finally made. Further study of his data by Tanton indicated that the mice did not learn to avoid the traps, but nevertheless the probability of capture was not the same throughout the population. The accuracy of results from use of Brass's (1958) method seemed to be reasonably satisfactory to Tanton.

Eberhardt, Peterle, and Schofield (1963) and Edwards and Eberhardt (1967) also have developed methods for estimating population density from frequency-of-capture, but they assumed the population fitted the geometric distribution. The latter is similar to a negative binomial one; a succession of Bernoulli trials is conducted and the investigator estimates the probability that k failures precede the rth success where r = 1; or to put it another way, the investigator estimates the probability that one success (the first one) would occur is $p\,q^k$ (Feller, 1957:155-156).

The paper by Edwards and Eberhardt discusses several methods for estimating population size by frequency-of-capture, based on a geometric distribution model, of which one of the most satisfactory ones was said to be derived from Hartley's (1958) procedure for maximum likelihood estimation where the the data are incomplete and a truncated sample has resulted; Hartley mentioned that his approach was similar to the missing-plot technique used in analysis of variance. Several of Edwards and Eberhardt's methods involved plotting the capture frequencies and fitting regression lines. After Hartley's approach was somewhat altered by Edwards and Eberhardt (1967), the following maximum-liklihood estimate, based on the geometric distribution, was obtained:

$$\hat{N} = \frac{\Sigma n_x}{1 - (\Sigma n_x / \Sigma x n_x)}$$

The symbols above are those used by Edwards and Eberhardt and mean the following: $\Sigma x n_x$ = the total number of captures (without regard to how many of the captures represent animals caught once, or twice, or some other number of times); Σn_x = the total number of different animals captured; $\hat{N}$ = the estimated total number of different animals in the whole population (or component studied).

Edwards and Eberhardt (1967) used a number of methods to estimate the abundance of cottontail raibbits (*Sylvilagus floridanus*) on two closely studied areas, including one a pen of 40 acres, and they found that the "geometric models" gave good results, particularly the equation shown above and a regression model. Multiple marking (with recapture) gave decided underestimates. Nixon, Edwards, and Eberhardt (1967) tested various procedures on several populations of tree squirrels (*Sciurus carolinensis* and *S. niger*) and concluded that both of the geometric models of Edwards and Eberhardt just mentioned gave useful results, whereas some procedures based on multiple marking (with recaptures) again yielded underestimates.

The proliferation of methods continues; appearing recently is a paper by Bennett (1957) giving a model rather related to the frequency-of-capture ones and yet not requiring the direct estimating of any missing class. Individual broods of ducks had to be identified during repeated sampling, and the number of

brood-sightings that were new were then plotted against the cumulative total of all previous sightings. After enough observations were made, said by Bennett to be reached when the ratio of new sightings to the cumulative total of earlier ones was near one-half, this gave a curve that tended to an asymptote. A logarithmic-series curve was fitted and the point estimated where enough total sightings would have been made to have yielded essentially the last newly observed brood. In effect, it appears to me, the size of the "zero class" is estimated indirectly at the point where it practically vanished; this is the point where nearly all of the unseen animals have been converted to observed ones. Confidence limits were not provided.

Relation of Variance to Mean

Hanson and Chapman (in press) have developed an estimator considerably different in principle from others discussed here because the method does not require that any population component be in effect positively identified by marking, removal, or total counts on sample plots (in principle an identification). On the contrary, rapid, cursory, incomplete counts are made repeatedly on an entire study area and the observed number of groups, and individuals within the groups, are recorded. Some convenient number, say 20 to 50, of rapid surveys are made under conditions as uniform as possible. The main assumption behind the procedure is that the data on number of groups for a binomial distribution, requiring among other things that each group will be seen or not, that the probability of observation is the same from group to group of animals and survey to survey, and that the observations are independent (clumping of groups not noticable). A secondary assumption is that the number of animals living on the study area remains nearly constant during the period of surveys.

It is well known that in a binomial distribution the product $k_g\ p_g$ is estimated by the mean, $\overline{x}_g$, where k_g is the actual total number of groups of animals livin gin the study area, p_g is the probability of observing them during cursory, incomplete counts, and $\overline{x}_g$ is the mean number of groups seen. It is also well known that the binomial variance, $k_g\ p_g\ q_g$, is estimated by s_g^2; q_g is defined by $1 - p_g$ and therefore is the probability that any given animal will not be seen during the incomplete counts. The expression for the variance can be divided by the one for the mean,

$$\frac{k_g\, p_g\, q_g}{k_g\, p_g} = \frac{s_g^2}{\overline{x}_g},$$

which after cancellation of like factors and replacement of q_g by $\hat{q}_g$ of course gives

$$\hat{q}_g = s_g^2 / \overline{x}_g\,;$$

from this it immediately follows that $\hat{p}_g = 1 - (s_g^2 / \overline{x}_g)$. Since $p_g\, k_g = \overline{x}_g$, and thus $k_g = \overline{x}_g / p_g$, the expression given for p_g in the preceding sentence is substituted into this latest equation to finally yield

$$\hat{k}_g = \frac{\overline{x}_g^2}{\overline{x}_g - s_g^2}.$$

Thus, a moment estimator of the density of the animal groups is established, and multiplication of the estimated number of groups, $\hat{k}_g$, times the average number of animals seen in each group gives an estimate of the total population of the study area.

Confidence limits for the above model, based on an approximation from the chi-square distribution, were derived by Dr. Chapman (Hanson and Chapman, in press). Both the confidence limits for the groups as well as limits for the individuals within the groups must be found and used jointly to find the upper and lower bounds for the estimated total individual animals on the study area. Although the equations for confidence limits are fairly easy to use, an adequate description of them would require more space than is practical in this review.

The model was tested considerably on laboratory populations of mealworms (*Tenebrio molitor*) (Hanson and Chapman, in press). In general, the method did not work very well, mainly because the mealworms had a highly contagious distribution, part of which was caused by the worms "piling up" in the corners of the pans; even the use of the number of groups, rather than merely of total individuals seen, did not seemingly permit a close enough fit to the required assumptions of the binomial distribution. When sample size was as big as 30 to 35, the results were of course better than in trials where only 15 or 20 counts were made. Since in nature groups of animals should tend to be distributed more at random than individuals are, the model may have use in some situations and should be tested further.

The estimator just reviewed can now be compared to the one of Seierstad *et al.* (1967) mentioned in the section on "Total Counts on Sample Plots." Evidently the models are the same or closely similar, although the one of Seierstad *et al.* does not show all of the steps in the derivation. Some of the main ways in which the Seierstad paper differs is that (1) the confidence limits appear to be derived differently (but further study by a statistician will be needed to clarify the point), (2) the model was designed to determine the efficiency of surveys giving total counts, (3) use of the number of groups to circumvent partially the problem of clumping was not mentioned, and (4) empirical testing of their model was not mentioned.

The only other sampling method known to the writer that yields estimates of density without requiring total counts, marking, removal, or other measures leading to positive identification of all of the animals in some group, is the flushing-count method of King (1937), which was revised and improved by Hayne (1949b). Although the procedure has many interesting and valuable features and has had considerable use, it will not be described further except to mention that it is based on (1) the number of animals that are seen to run or fly from the observer as he walks along a predetermined survey-line and (2) the average distance between (a) the observer and (b) the spots where the flushed animals are first seen. King's method is thus not based on the statistical distribution of data in the sense that other papers covered here have been.

Summary of Models Based on Fitting of Distributions of Data

The frequency-of-capture methods require that individual animals must be marked or otherwise made identifiable, and this necessarily causes many of the potential shortcomings of other methods requiring marking. The model based on the interrelations of the mean and variance is nearly unique because no component of the population need be captured, removed, or otherwise made identifiable, either individually or as a group (as happens in principle when total counts are made on sample plots), and thus the data can be gathered more easily. All of the models covered in this section suffer from the following difficulties: (1) Probability of capture or of field observation may not be the same for all of the animals or their groups; (2) population density may change during the period of study; and (3) the data obtained may not fit the assumed underlying distribution.

Southwood (1966:88-89) claimed that any of the procedures discussed in Craig require the animals to be exceptionally mobile "so that their chances of recapture are virtually random almost immediately after release," and thus he concluded that the methods have limited possibilities except for "large conspicuous flying or very mobile animals under certain circumstances." I do not regard his reservations as being entirely warranted, however, because the time between captures need not be any shorter than they are in the multiple marking scheme. When an animal is captured on a given day, marked, and released, its presence can be ignored for the remainder of that day if it should happen to be caught again, or it can be ignored for longer periods. This will give it sufficient time to distribute itself randomly within the population. In other words, all of the initial encounters with the various trapped animals during one day (or a small number of successive days) can be treated as one sample all caught at the same instant. This sample can be compared to all of the initial encounters on a later day (or small group of days). By initial encounters is meant the first capture of a given animal on a given day, regardless of how many times it has been captured on earlier days. In general, the collection of valid data for the frequency-of-capture methods should not any more difficult than it is for the Dahl (Petersen) mark-and-recapture techniques.

The prospects for getting the proper data to fit the (positive) binomial method of Hanson and Chapman (in press) seem least likely. Prospects are better for Hovanitz's model (Method 2 in Craig, 1953) based on the Poisson distribution. The required assumptions for the data are even more likely to be met by the negative-binomial procedure of Tanton (1965) and the geometric method of Edwards and Eberhardt (1967). However, all of the methods based on the statistical distribution of the data have been tested so little in the field that it is not possible as yet to say which has greater value, although the model of Edwards and Eberhardt appears to hold most promise. Nevertheless, if some day sound methods could be developed for estimating population density from rapid, cursory, incomplete counts of free-ranging animals, this would greatly lighten the labors of the population ecologist.

CONCLUSIONS AND SUMMARY

This relatively brief survey of the rather enormous literature on population estimation indicates that many procedures are available but all of them contain pitfalls. Evidently there is not a "best" way to estimate population density for animals in general, because each population is unique in theory and in actuality, and each estimating procedure has strong and weak points. Although each one given population has continuity in time, it varies more or less continually. Results from estimating procedures are importantly affected by the biology of the animals, especially their ecology with its changing environmental influences. Therefore, the investigator who needs to estimate density should have in his repertoire numerous procedures to meet the variable ecology of the animals. Moreover, if density in any one time-period and place is estimated by several procedures, the worker can determine if the results obtained are nearly the same. If they are not, the work should be repeated and possible additional procedures should be invoked.

Although a number of papers have been cited herein, many were considered only slightly, and many more valuable writings on the subject were not even mentioned, whether by accident or intent. Additional papers on the subject roll off the presses monthly or weekly, and some represent marked departures from older procedures. The trend toward more models and greater testing of them should continue, and it will bring slow but sure gains in one of the ecologist's most diffiicult jobs, the estimation of population density.

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